CHAPTER V

THE MECHANISM OF ASSORTMENT

EACH pair of chromosomes, just before the reduction division, consists of a maternal and a paternal member. As the members of each pair are in nearly all cases identical in appearance, it is not possible to tell how they place themselves on the mitotic spindle with respect to their parental origin; that is, it is not possible to tell by inspection whether at the maturation division all those of maternal origin pass to one pole of the spindle, and all those of paternal origin to the other, or whether the pairs come to lie haphazard on the spindle, so that it is merely a matter of chance whether a maternal or a paternal member passes to a particular pole. For the utilization of the chromosomal mechanism for the theory of assortment, it is a matter of great importance which of the preceding alternatives is followed, for if all of the maternal chromosomes should go to one pole, and all the paternal to the other, there would be no free assortment of the chromosomes, and no free assortment of the genes if these are carried by the chromosomes. Without random assortment there could only be two kinds of gametes produced by the hybrid, hence only three types possible in F_2, viz., the two grandparental types and the hybrid type.

On the other hand, if the assortment of chromosomes is a random one, then the reduction division furnishes the mechanism that Mendel's law calls for in so far as the character-pairs lie in different chromosome pairs.

There is not a single cytological fact opposed to the view of free assortment of maternal and paternal chromosomes; on the contrary, there is a general expectation that the chromosomes should assort freely; and what is more to the point, there are a few crucial cases that show that free assortment takes place. Let us turn to these

cases.   The most convincing evidence is that furnished
by Miss Carothers (1913) from some grasshoppers of the
genus *Brachystola*.   Here, in addition to the single sex-
chromosome (in the male), that goes to one pole of the
first maturation spindle, there is also present another pair
of chromosomes that are unequal.   In some cells the
smaller member of the pair goes to the same pole as the
sex-chromosome, in other cells it goes to the opposite
pole.   The assortment of the unequal pair as regards the
sex-chromosome is therefore a random one.   Thus, in
three hundred first spermatocytes, the smaller partner
went to the same pole as the sex-chromosome in 48.7 per
cent. of cases, and into the cell without the sex-chromo-
some in 51.3 per cent.   Voinov ('14), Wenrich ('14) and
Robertson ('15) have reported similar cases.

Other evidence of a different kind has more recently
('17) been described by Miss Carothers.   The evidence
rests on the constancy of attachment of the fibres of the
mitotic figure to a definite point of the chromosome, as
seen when the chromosomes are moving towards the poles
of the spindle.   In one of the cases she describes there
are two kinds of attachments, *viz., terminal,* when the fibre
is attached at the end of the rod-shaped chromosome, and
subterminal when the fibre is attached some distance from
the end.   In the latter case the end bends over, making
the chromosome J-shaped.   There are certain individuals
in which one member of a pair of chromosomes may have
a terminally attached fibre, and its mate have a subter-
minally attached fibre.   Throughout all the cell-divisions
of such an individual these two chromosomes show this
difference.   During maturation, *i.e.,* after conjugation of
the chromosomes, one member of this pair passes to the
pole of the spindle with a terminal attachment, and its
mate with a subterminal to the other pole.   In the male, the
single sex-chromosome passes to one or to the other pole
at one spermatocyte division.   Its relation to the two
members of the pair of chromosomes in question will show

whether random assortment or correlated movement takes place. Observation shows that sometimes one, sometimes the other, member of the pair goes to the same pole as the sex-chromosomes.

It happens that in a species studied by Miss Carothers (*Trimerotropis suffusa*) there are several chromosomes that may show constantly terminal or subterminal attachment of the fibres; as many as seven out of the twelve chromosomes of the first spermatocyte division may consistently show this difference. In other words, any one of these seven chromosomes may have one or the other kind of attachment. Each grasshopper may have any one of ten of its pairs showing combinations of these kinds of attachment, but of course in any one individual only two possible arrangements exist for a given pair of chromosomes. It is to be remembered that for a given combination all the cells of an individual are exactly alike, which incidentally is a strong argument in favor of the individuality of the chromosomes. An example will give further details. In Fig. 32 are shown eight groups of chromosomes (b, c, d, e, f, g, h, j) from the same individual. Each group of 12 chromosomes comes from a single cell about to divide. Each series of 12 is here arranged in a single horizontal line. The dividing chromosome is a tetrad, one of whose halves is about to separate. It is significant to note that in this case the separating halves represent the two conjugating members of each pair; in other words, the *reduction* division is taking place. In this individual, four of the tetrads (9-12) have subterminal attachment only, *i.e.*, for both members of the dividing pair (dyad); four of the tetrads (Nos. 2, 3, 5 and 6) have terminal attachments only, while the remaining three tetrads (Nos. 1, 7 and 8) have one end with a terminal attachment, and the other subterminal. In addition there is the sex-chromosome (No. 4) that is here going upwards toward the top of the figure, and will pass with the upper half of each tetrad into an imaginary cell above (the female-

producing sperm). The first double chromosome (No. 1) has a different mode of fibre attachment to each half, but the halves are here not different in size. In five cases the chromosome with terminal attachment is going to the cell that will get the sex-chromosome (the upper one here), while in three cases it goes to the pole that will not get the sex-chromosome. Chromosomes 7 and 8 are slightly different in size, but this is not distinguishable in these figures. In the first four cells (*viz.*, *b, c, d, e*) the halves of 7 and 8 with subterminal attachments are going to opposite poles; in the remaining four cells (*f, g, h, i*) they are going to the same pole. Again, if we compare Nos. 7 and 8 with No. 1 it is found that in four cells (*f, g, h, i*) the half with terminal attachment passes into the cell with the same attachment (*f* and *i*) (for 7 and 8), and the other half into the cell with the other attachment (*g* and *h*). In other words, the distribution for four chromosomes pairs (1, 4, 7, 8) is here a random assortment. Let A, B, C represent the chromosomes with one kind of attachment, and *a, b, c* their mates with the other kind of attachment. D is the sex-chromosome and *d* its absence. There will then be sixteen possible assortments of these four, all equally probable. Thus:

$$\begin{array}{ccccc}
ABCD & aBCD & abCD & abcD & abcd \\
& AbCD & AbcD & abCd & \\
& ABcD & ABcd & aBcd & \\
& ABCd & aBcD & Abcd & \\
& & aBCd & & \\
& & AbCd & &
\end{array}$$

There were 100 spermatocytes recorded by Miss Carothers as to the distribution of their chromosomes to the two poles, giving data for 200 cells. Their distribution as well as the expectation for free assortment is as follows:

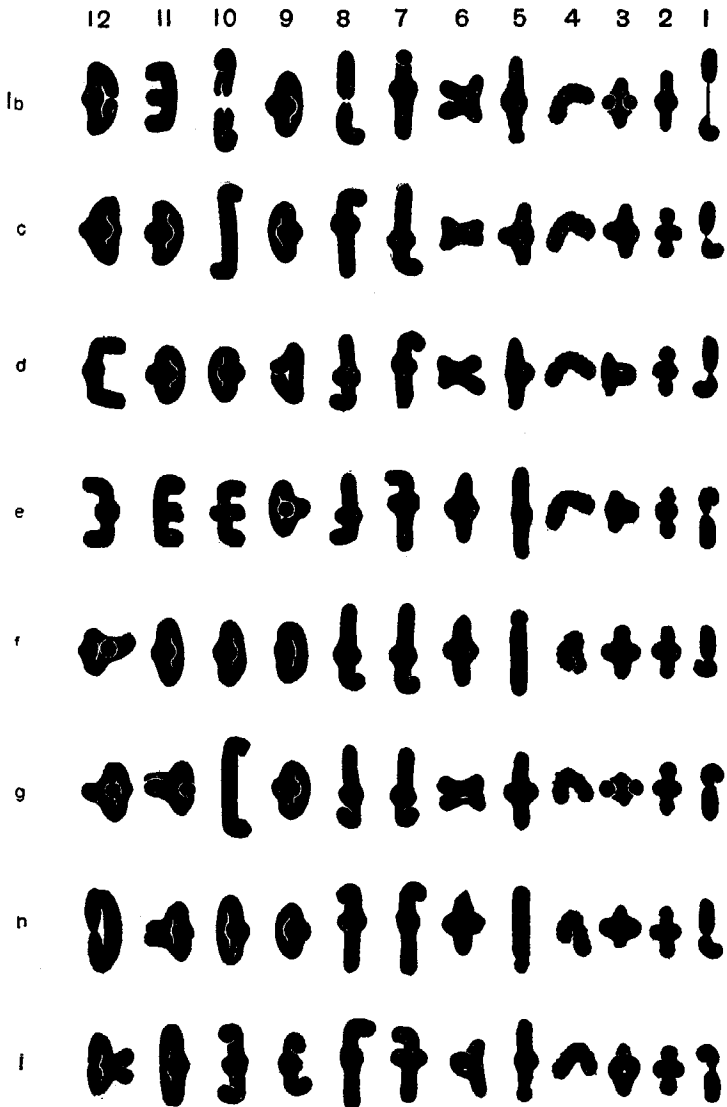|	Expected	Realized
Only one chromosome with sub-terminal attachment.	$\frac{1}{4} \times 200 = 50$	48
Any two chromosomes with sub-terminal attachment.	$\frac{3}{8} \times 200 = 75$	84
Any three chromosomes with sub-terminal attachment.	$\frac{1}{4} \times 200 = 50$	48
All four chromosomes with sub-terminal attachment.	$\frac{1}{16} \times 200 = 12\frac{1}{2}$	8

FIG. 32.—Eight chromosome groups of twelve chromosomes each of *Trimerotropis*. (After Carothers.)

For a count of only 100 cells the agreement with expectation is sufficiently close to show that independent assortment takes place.

In addition to the differences of attachment just examined there are other differences that Miss Carothers has studied. A constriction is found in certain chromosomes in some individuals (Fig. 32, No. 5) that is absent in other individuals. In some individuals the tetrad is separating so that the group looks like four beads in a line. In other cases one member of the pair is not constricted, while its mate is constricted. Similarly for another chromosome. In one individual both halves of the dyad show a constriction, while another individual has one smooth and one constricted half. These same two kinds of chromosomes also have in some cases terminal attachment, and in other cases subterminal, making possible further combinations that can be identified.

Finally, there are two types of subterminal attachment in two chromosomes of the series. In one type the chromosome is bent further from the end than in the other. Either of these two types may have a mate of the other type with terminal attachment, thus giving several further identifiable combinations. "All possible combinations of the dyads in these two types of heteromorphic tetrads occur and segregate [assort] freely in relation to sex." Miss Carothers points out that when three types of the same chromosome exist "we have a visible mechanism whose behavior in the maturation divisions corresponds to the segregation of triple allelomorphs."

In addition to the 12 ordinary chromosomes certain individuals may have a small thirteenth or even a fourteenth chromosome. These are called supernumeraries. In *Circotettix* they were found present in two of eleven individuals examined. If present, it, or they, are constant for all cells except that at the reduction division there may be a new distribution. If one is present it may go to either pole with reference to the sex-chromosome, and at

the second spermatocyte division it divides as do the others at this time in the cell that contains it. If two are present they do not behave as mates, but at the first spermatocyte division may both go to the same pole (which may be either pole in reference to the sex-chromosome), or they may go to opposite poles. At the second spermatocyte division each divides independently, and halves go to opposite poles. These bodies then also move to either pole without respect to other chromosomes—or at least without respect to the sex-chromosomes; but this behavior can scarcely be used to advantage for the question of assortment because these chromosomes have no mates (in the cases so far described) and are so inconstant in their occurrence that an appeal to their behavior as bearing on the other chromosomes might not be conceded. If they are pieces of other chromosomes (the bent ends, for example) that have been broken off, we might expect them to show some relation during synapsis to the original chromosome from which they came, but as yet nothing of the sort has been described. If they carry factors that influence the characters of the individual, their presence, especially when two occur, would give rise to unexpected genetic results.

The evidence furnished by cytology that has just been given makes clear that whenever an opportunity has been found to study the mode of assortment of the chromosomes the result shows random distribution. If then the chromosomes carry the genes for the hereditary characters, we should expect that the genes in different chromosome pairs will "assort" independently, and this, in fact, is what Mendel's second law postulates.